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**Pollination success of *Silene tatarica* in
different spatial habitats**

Bestäubungserfolg von *Silene tatarica* in unterschiedlichen Lebensräumen

Bachelor thesis to obtain the degree Bachelor of Arts in Biology

submitted by

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1. Introduction and questions

1.1 Reproduction in angiosperms and the role of pollination

In general the propagation process in angiosperms can be divided in sexual and asexual reproduction. Asexual or vegetative propagation takes place without recombination of gene material; cells are divided by mitosis. Organs of vegetative reproduction can be rhizomes, bulbs, runners, etc. In the sexual reproduction the gene material is recombined in each reproduction cycle with the help of meiosis and karyogamie. Some species may practice both models of reproduction; some are restricted to one way of propagation (Kück and Wolff, 2002).

Pollination is an important step in the sexual reproduction cycle of angiosperms. The process describes the procedure, when the pollen grain, which contains the male gametes (sperm), is transported from the anther to the carpel, containing the female gametes (ovule). The receiving part is the stigma (Dafni, 1992). Pollination is divided into three phases: First, the release of the pollen from the anthers, second, the transfer to the stigmas and third, the depositing of the pollen on the receiving part with the following germination of the pollen grain (Fig. 1). Pollination takes place during the anthesis; the time period when anthers and stigmas are exposed to the pollinating agents. The following steps in the reproduction cycle are the fertilization and the development of seeds and fruits. The developing seeds exhibit the resources for the new offspring (Fægri and van der Pijl, 1979). Figure 1 describes the three phases of pollination and the following steps in the reproduction cycle, including the measureable factors contributing to pollination success.

1.2 Self pollination

Many flowering plants have hermaphrodite flowers¹. Because of the closeness of male and female organs there is the chance of self pollination: The stigma of an individual receives its pollen from anthers that belong to the same individual. It is estimated that worldwide around 40 % of the plants are able to propagate by self pollination (Sitte, Weiler, Kadereit and Körner, 2002). In the majority of cases self pollination implicates self fertilization (autogamy).

¹ Flower that contains female and male organs.

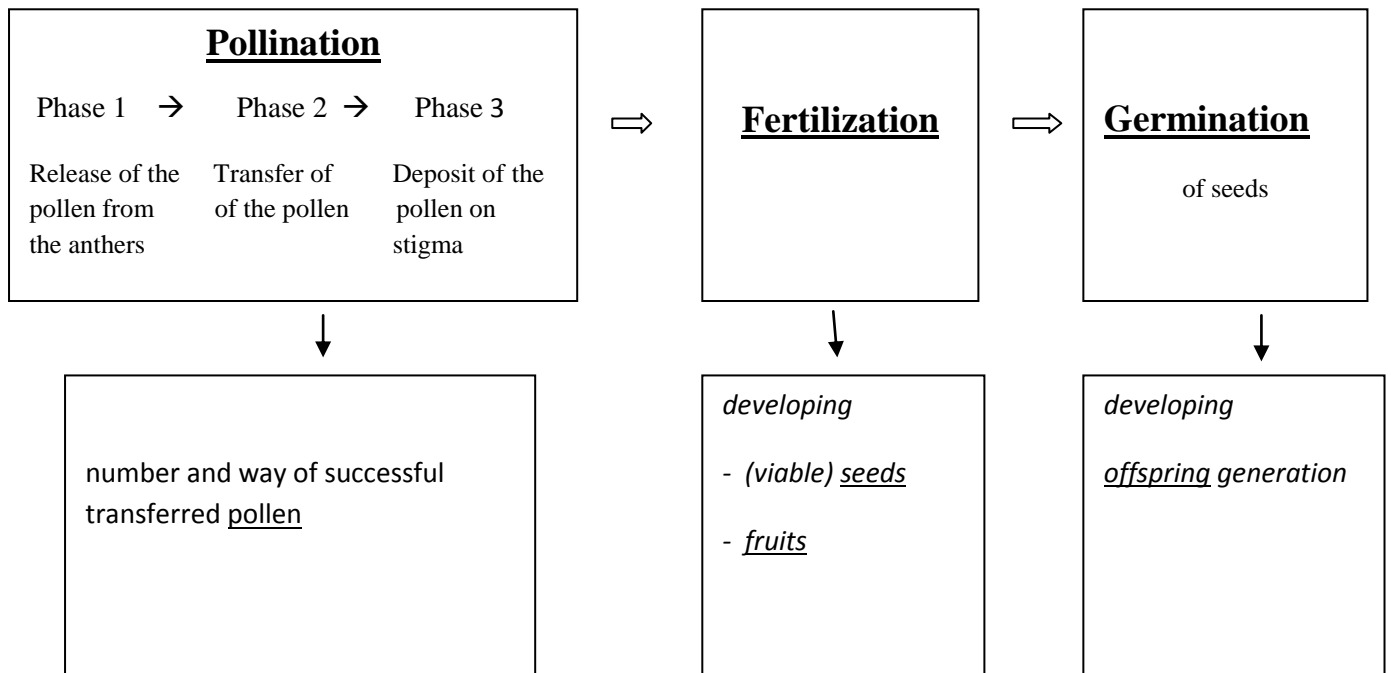


Fig. 1. Process of pollination and the following steps in the reproduction cycle (first line). Measureable factors contributing to pollination success within the steps (second line).

The pollination with the pollen of a neighbor blossom of the same individual is called geitonogamy. For populations, autogamy and geitonogamy have the same genetic effect, called inbreeding: The genetic variability of individuals, produced by inbreeding, decreases, because there is no crossing among different individuals. At long sight, this effect inhibits the development of new characteristics that may be favored by selection (Fægri and van der Pijl, 1979).

To avoid self pollination and thus, self fertilization, some plants are self incompatible. It is estimated, that 50 % of angiosperms exhibit such a self incompatibility system (Sitte et al., 2002). Within these plants the successful transfer of pollen does not result in successful pollination because of barriers that occur during or after the pollination (Fægri and van der Pijl, 1979). Many plants have developed some traits to avoid self pollination, for example dioecy² or protrandry³ (Sitte et al., 2002). Self pollination is sometimes the only possibility to propagate for some individuals. On islands or extreme habitats, where pollinators are absent, inbreeding species often grow successfully, for example. Furthermore it is estimated that within many species there is a certain degree of self pollination to reach the optimal

² Individual produces either only male organs or only female organs.

³ Male function precedes female function.

pollination success. The degree can differ among populations, depending on habit type etc (Fægri and van de Pijl, 1979).

1.3 Cross pollination

Genetic heterozygosity can be increased by out crossing. The most plants of angiosperms exhibit cross pollinated flowers. The stigma of one individual is pollinated by the pollen of another individual (xenogamy). Outbreeding is favored by selection; the produced individuals exhibit a greater genetic variability and conditions require environmental selection among diverse genotypes (Fægri and van der Pijl, 1979).

The ways of transporting the pollen from one plant to another varies among pollination systems. One option is the abiotic pollination: The pollen are transferred by external environmental influences, like wind (anemophily) or water (hydrophily). Anemophily, the dominant type of abiotic pollination (95-98 %), occurs predominant within the gymnosperms, but also within the angiosperms; mainly in the families of Poaceae, Cyperaceae, Juncaceae and Fagaceae. Hydrophily particularly occurs in hydrophytes, like *Zostera marina* (Dafni, 1992). Beside there is the biotic pollination; which is discussed in detail in the next chapters.

1.3.1 Pollinators

The biotic pollination requires the presence of a second organism; an animal that transports the pollen. The animal touches the blossom, leaves the plant with the pollen attached to its body, lands on another plant and leaves the transported pollen particularly there. Plant-pollinator relationships evolved in the course of time and are typical examples for coevolution. With the help of pollinators, plants are able to increase their out crossing rate and an improvement in reproduction success (Schowalter, 2006). From the pollinator's view the relationships are attractive because the plants provide attractants as the pollen themselves, nectar, oil, etc. (Leins and Erbar, 2008).

The biggest group of pollinators is represented by insects (Leins and Erbar, 2008), but there are also some bird pollinated (hummingbird pollination) or bat pollinated plants, particularly in the tropes. According to their feeding behavior Schowalter (2006) divides the insects in pollen feeders and nectar feeders. Pollen feeders are mainly bees, bumble-bees,

beetles and thrips; they transport the pollen during feeding. While the nectar feeders like bees, bumble-bees, beetles, butterflies, moths and flies are primarily interested in the nectar and transport pollen more coincidentally. The meaning of ants in the role of pollinators is still controversial, but probably they are less important to pollination (Schowalter, 2006). Beside the feeding behavior pollinators differ also among their time of activity. Especially moths are night active animals, which visit plants predominant at night, while the other insects pollinate flowers mainly at day (Leins and Erbar, 2008).

1.3.2 Plant-pollinator interactions

The interaction, abundance and visitation rates between plant and pollinator, determines the effectiveness of pollination. There are many different factors which influence these interactions. In the course of time pollinators developed certain characteristics, as mouthparts or body size, that predicts them to pollinate special species (Schowalter, 2006). Furthermore pollinators differ in their pollination behavior: There are pollinators visiting certain plant species frequently and there are pollinators visiting a plant only once accidentally (Fægri and van de Pijl, 1972). According to the pollinators, there are also evolutionary evolved plant adaption characteristics: Nectar, floral and nectar advertisements, floral structures, only day or only night flowering plants, etc. (Schowalter, 2006).

Extreme adaption causes specialization: The more the pollination system is specialized the more the diversity of different pollinators per species decreases. According to Fægri and van der Pijl (1972) specialization has two sides: It can encourage visits from certain animals, and therewith the pollination efficiency. Specialization is favored by selection, if the most abundant pollinators are also the most efficient pollinators (Waser, Chittka, William and Ollerton, 1996). A disadvantage of this interdependence is the weakness which is shown, if one of the partners disappears. Long, narrow tubes, that can be found in butterfly blossoms for example, amplify butterfly visits, because they can reach the nectar with their proboscis, but exclude pollinators without these mouthparts (Fægri and van de Pijl, 1972). Beside this specialization, in many plant pollination systems a diversity of pollinators can be seen. These plants show a generalized pollination system. The plants do not depend on one pollinator species directly. It has been proven that the most successful colonizers exhibit generalized pollination systems (Fægri and van de Pijl, 1972).

Moreover the plant-pollinator interaction depends on the habitat type where the population occurs: Bell and Lechocwicz (1991) found that environmental variation can cause

differences in fitness-related plant traits, such as time to maturity, germination time, height, root mass and shoot mass (Bell and Lechowicz, 1991). These characteristics may influence the visitation reference of pollinators. Beside this, abiotic factors, such as light intensity, can influence the presence of pollinators or plant population characteristics, such as density or number of inflorescences (Grindeland, 2005). The result is that populations of the same plant species, which occur in spatial separated habitats, can be exposed to different pollinators and pollen availability (Hansen and Totland, 2006). Figure 2 gives an overview about the factors, which can influence the plant-pollinator relationship.

While pollination contributes to the reproductive success of plants, insect visits are not always of advantage for the plant. Seed and fruit predation are phenomena characterizing some plant-animal interactions, too. As an example, seed predators consume the seeds and reduce the plant reproductive efficiency. Another example is nectar robbery; some nectar feeders avoid the reproduction organs by perforating the bottom of the flower to reach the

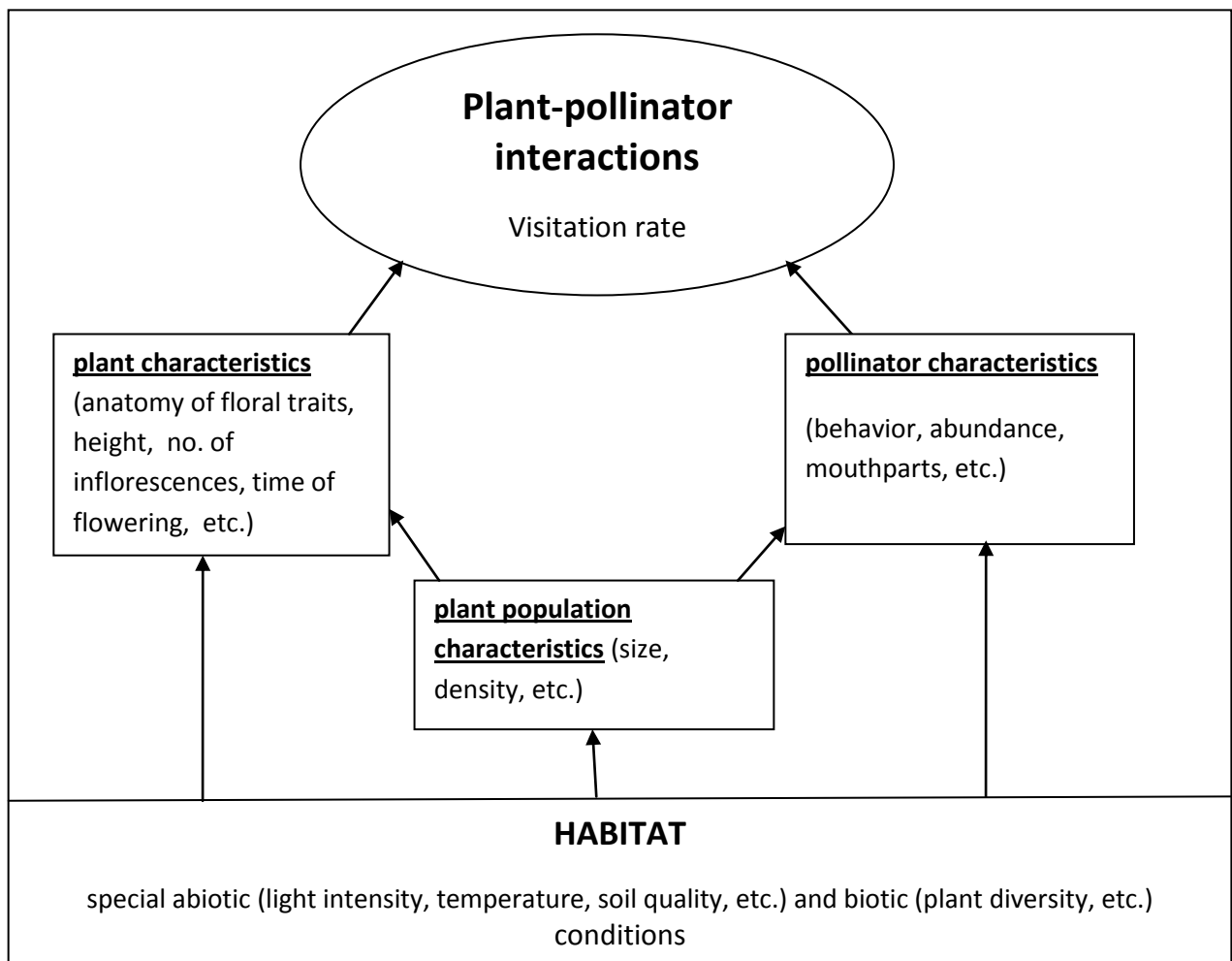


Fig. 2. External influences on plant-pollinator interactions.

nectar (Dedej and Delaplae, 2004). Pollinators can decrease the reproduction success, too, the *Silene-Hadena* interaction (1.5), for example.

1.4 Pollination success: How can it be measured?

Successful pollination induces fertilization and the maturation of seeds. From the reproductive's point of view, the production of viable seeds determines the pollination success (Fig. 1). Viable means, the ability of seeds to germinate to a new plant; the offspring generation can give final information about the quality of the seeds (Dafni, 1992). The process of biotic pollination is strictly connected to the pollinator's behavior, thus there is a big interest in the pollinator's visitation rates and their influence on fruit and seed production. In many studies pollinators are observed to get detailed information about their pollination effectiveness. There are two major factors determining the effectiveness of pollinators, first, the relative abundance of pollinator and second, the rate of removing and depositing pollen (Young, 2002). To estimate the exact stages of the pollination process (Fig. 1) the pollen grains and their way must be analyzed, with the help of dye, for example. The number of transferred pollen differs with each pollinator, and not all of the pollen, removed from the anthers, are deposited on stigmas of the same species. Moreover it must be seen that a certain amount of pollen must be deposited on the stigma for the development of seeds.

After fertilization, the fruit set, the number of flowers that set fruits, is a first indicator to estimate the effectiveness of pollination and pollinators. The number or quality of fruits may be due to the source of the pollen with which the ovules were fertilized (Fenner and Thompson, 2005). Furthermore the number of fruit set is a good estimator for the direct comparison of the activity of certain groups of pollinators and hence their effectiveness, for example day vs. night pollinators. Finally, the viable seeds are the best indicator to estimate successful pollination (Dafni, 1992). The more viable seeds the bigger the resource for an offspring generation. A viable seed should show advantageous characteristics and structures for dispersal and survival (Fenner and Thompson, 2005). Then it must be seen that there might be a trade-off between seed number and seed size. Within each species there is an optimum to produce the adequate seed mass per fruit, with the smallest amount of defective seeds as possible. Seed number and size vary among the species and depend on the environment and circumstances extremely (Fenner and Thompson, 2005).

These factors can be summarized to the "female reproductive success" and "male reproductive success" that determine the pollination success: The number of the deposited

pollen grains on stigmas, fruit set and the seed set belong to the female reproductive success. The male reproductive success contains the pollen removal, the distance of the pollen removal and the success of pollen on stigmas of conspecifics (Young, 2002).

1.5 Pollination and pollinators in the taxon of Caryophyllaceae

Pollination biology is a widely studied theme within the taxon of Caryophyllaceae and plant-pollinator interactions within this taxon differ among the species. The genus *Silene* (Linné) with its 700 species is one of the largest genera worldwide and occurs on all five continents (Greuter, 1995). The most species are entomophil⁴ and pollinated by animals, but for plants occurring at windy areas, wind pollination can sometimes contribute to fruit set (Norman, Weller and Sakai, 1997). Autogamy occurs in some species of the genus *Silene* (Jürgens, Witt and Gottsberger, 1996). In contrast, some species developed barriers against self pollination, for example *Silene alba* (Poiret) [= *Silene latifolia* (Miller) Krause = *Silene pratensis* (Spreng) Gren. & Godr; = *Lychnis alba* Miller; = *Melandrium album* (Miller) Garcke], as a dioecious plant (Young, 2002), or *Silene lemmonii* (Watson) with its protandrous flowers (Hove, 2007). Among the genus *Silene*, the plants differ in flower colors, flower orientation to pollinators, petal sizes and shapes and nectar- and scent production (Buide, 2005).

Most of the species are visited by several pollinators; one big issue concerns diurnal vs. nocturnal pollinators and hymenopterans vs. lepidopterans. Kephart (2006) estimated that for 56 % of the Caryophyllaceae lepidopterans are the major pollinators and still 29 % are mainly pollinated by bees. Nocturnal pollinating lepidopterans are particularly represented by moths, and they occur mainly in Europe and North America. Bees, especially bumble-bees, are the most common diurnal pollinators (Kephart, 2006); they may also visit moth pollinated plants. The importance of bees and also butterflies is difficult to estimate because it varies extremely on a temporal and spatial scale. Other common pollinators are flies, especially hover flies, and bee flies; they visit many different species within the Caryophyllaceae. Also some dipterans visit plants of Caryophyllaceae, but their contribution to the pollination efficiency is still unknown (Kephart, 2006). Some species are pollinated by certain species of moths: *Hadena* and *Perizoma*. These moths take a role as parasitizing pollinators: Imagines may visit the plants and transfer pollen, but they also leave their grubs in there. The larvae grow protected within the developing fruits and decrease the seed production (Kephart, 2006).

⁴ Blossom adaption to its pollinators.

It is still questionable if these visitors contribute to pollination or reduce the reproductive success of plants (Giménez-Benavides, Dötterl, Jürgens, Escudero and Iriondo, 2007).

The determination of pollinators and their behavior on plants base on observations. The contribution of diurnal and nocturnal pollinators to pollination success is often estimated by a pollinator exclusion experiment, as it is adopted in this experiment (2.3). Giménez-Benavides et al. (2007) observed visitors of *Silene ciliata* (Pourr). Although it is specialized to nocturnal pollinators, with its pale flowers that open at dusk and emit an intense scent at night, it is also pollinated by diurnal pollinators. Giménez-Benavides et al. (2007) analyzed a direct coherence between pollinators and seed production, fruits resulting from pollination by nocturnal pollinators produced a higher brood size than others. Young (2002) analyzed the pollination system of *Silene alba*, also a species that shows a nocturnal pollination syndrome: The dioecious plant opens the flowers at night. She found that the most produced seeds result from pollination by nocturnal pollinators (moths). Diurnal pollinators (bees, wasps and flies) contributed less to seed production. Overall, she suggested the pollinator effectiveness is greater for moths than for diurnal visitors (Young, 2002).

1.6 Goal of this study

As it can be seen pollination systems of species within the Caryophyllaceae differ extremely. This study is supposed to analyze the pollination biology of one special species, *Silene tatarica* (Linné). To the authors knowledge there are rarely previous studies about the pollination biology of *S. tatarica* and its pollinators. This study follows two main goals. The first aim is to analyze the differences of pollination success among populations of *S. tatarica* that grow in different environmental habitats in northern Finland. It should be found how population's pollination success depends on spatial habitat conditions and how these habitats influence the plant-pollinator interactions.

Hypothesis 1: The habitat type influences the pollination success of spatial populations of *Silene tatarica*.

The other big issue regards the process of pollination more detailed. According to pollinators of other species of *Silene*, it is suspected that *S. tatarica* shows a relatively generalized pollination system; it might be pollinated by several pollinators. It should be estimated the contribution of diurnal and nocturnal pollinators to female reproductive success

in *S. tatarica*. Furthermore the degree of self pollination in the pollination system of *S. tatarica* is regarded.

Hypothesis 2: - *Silene tatarica* is pollinated by more than one species and there are diurnal and nocturnal pollinators which contribute to pollination success.

- There is a certain degree of self pollinated flowers in successful pollinated plants of *Silene tatarica*.

This is a matter of a pilot study, because there are no pollination studies about *Silene tatarica*. This work is supposed to check the used methods, whether they are useful to study the pollination success and the pollinators of *Silene tatarica* or not.

2. Material and methods

2.1 Study species and study area

Silene tatarica (Caryophyllaceae) is a rare, perennial herb that lives on average seven to nine years (Rothmaler, 2005). The main distribution area of *S. tatarica* is located on Russian steppes, with disjunctive occurrences in Hungary, Germany, Lithuania and northwest Russia (Aspi, Tuomi, Jäkäläniemi and Siikamäki, 2002). There are also some populations in northern Finland. These populations can be found along riverbanks, sand and gravel shores of the Oulanka river. One individual is on average 30 cm to 60 cm tall and has several vegetative and fertile shoots with terminal inflorescences (Fig. 3a). *S. tatarica* commands deep, resilient tap roots (Jäkäläniemi, Kauppi, Pramila and Vähätaini, 2004). The plants are in flower from the end of July to the middle of August and individuals reproduce the first time in their third summer (Aspi et al., 2002). The plants have small, white blossoms (Rothmaler, 2005) (Fig. b).

One adult produces thousands of seeds during a growing season. The seeds are dispersed by gravity and water and start to germinate in the beginning of June (Aspi et al., 2002). Seedlings and young plants show a very high mortality rate, because they can hardly resist the environmental conditions (Jäkäläniemi, unpublished data).

a)



b)



Figure 3. Individual (a) and blossom in detail (b) of *Silene tatarica* in the Oulanka National Park. (Fotograph: Matt Brewster)

Adaption to the environment like special anatomic structures (vertical rhizomes, fleshy underground roots and shoots, etc.) enables the survival of plants that grow in disturbed habitats. Furthermore the flat tiny shape of seeds enhances the long-distance dispersal by water and gravity (Jäkäläniemi et al., 2004).

The study area is situated in the Oulanka National Park in northern Finland, in the highlands between Kuusamo and Salla, close to the Russian border (Aspi et al., 2002) (Fig. 4a). The study site is placed among the Oulanka river (66°N, 29°E), ca. 20 km south of the polar cycle. The boreal climate in these lines of latitude is characterized by cold winters and relative warm summers with some hot days. There is a thick snow cover from October to May, the growing season is short (Jäkäläniemi et al., 2004). During summer season the sun sets only for a few hours per a day (Schwartz, 2006).

The Oulanka river is a meandering river with sandy, gravel riverbanks and shores from erosion slopes to flat sand shores (Koutaniemi, 1984) (Fig. 5). From the end of April to the beginning of June flooding, caused by fast melting snow, prevents growing of plants by ice scour, floating dead trees, bank slumping and other incidents (Jäkäläniemi et al., 2004).

a)



b)

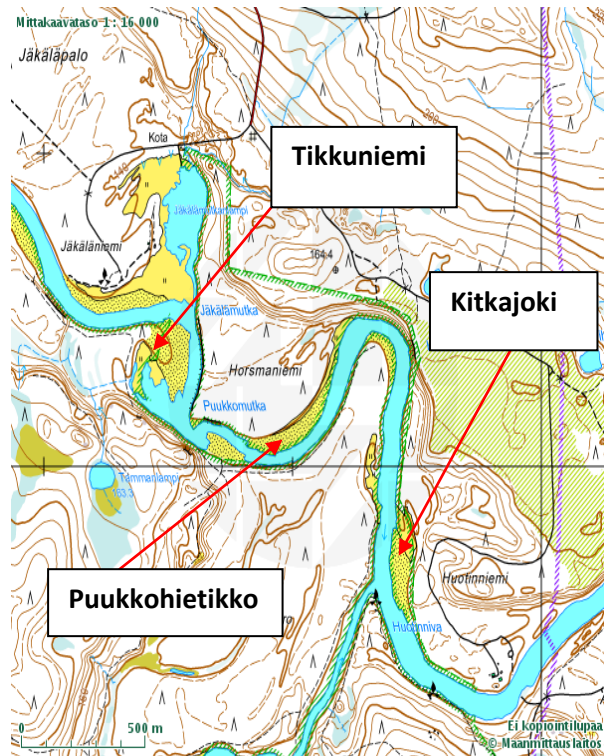


Fig. 4. a) Map of Finland and Oulanka National Park. b) Geographic location of the three habitat types.

The river valley is characterized by high variability in vegetation and rare plant species that depend on the habitat extremely (Saari, 1978). On the one hand, floods can easily destroy populations of plants, but on the other hand they also make new colonization possible (Jäkäläniemi, Tuomi, Siikamäki and Kilpiä, 2005).

2.2 Field methods

The measurements have not been completed by the author himself, Anne Jäkäläniemi and Matt Brewster designed the experimental design and completed the measurements. Plants of three different populations of *Silene tatarica* at different stretches of the Oulanka river have been analyzed (Fig. 4b). In the first population, 29 plants have been measured. The first population is situated at Puukkohietikko, a densely vegetated stretch of a valley of the Oulanka river.



Fig. 5. Oulanka river in the Oulanka National Park.
(*Fotograph: Matt Brewster*)

There are many other plants growing in this habitat. The second population is situated at a place called Tikkuniemi, a habitat that is sparsely vegetated, 28 plants have been analyzed there. Plants of the third population grow in an open area, Kitkajoki, a sandy gravel shore of the Oulanka river, the number of analyzed individuals is 27. Only a few plants grow there.

For the estimation of contribution of diurnal and nocturnal pollinators to pollination a pollinator exclusion experiment has been designed: Plants were enclosed with a net during certain time periods to exclude the pollinator groups. The net was put over the whole individual, and the mesh size was approximately 2 mm x 2 mm. Figure 6 shows an enclosed individual. There were four different experimental groups in each population: The first group was a control group; the plants within this group were not treated. The second group was the day pollinated group. In this group the individuals have been enclosed with a net during the night. The third group was the night pollinated group, the individuals are net treated during the day. The fourth experimental group was the self pollinated group. The plants were enclosed with a net day and night. The pollinator exclusion experiment took place during the flower period of *Silene tatarica*. It started in the beginning of August 2008 and lasted 10 days.

The following variables were measured in the beginning of the pollinator exclusion experiment: The height of each shoot and the flower number per shoot of each individual. In



Fig. 6. Pollinator exclusion experiment: Net treated individual of *Silene tatarica*.
(Fotograph: Matt Brewster)

the end of August, after the net treatment period, the seed containing capsules per shoot have been counted, as a further variable. Then one or several upper capsules of each individual has been chosen and the number of seeds have been counted. Furthermore they were divided in good and bad seeds. Good seeds had a kidney-shaped form and were expected to dispers and germinate well, while bad seeds were not. The good seeds were scaled. Table 1 gives on overview about the measured variables.

2.3 Statistical methods

2.3.1 Descriptive statistics

First the mean of the measured variables was calculated for each individual seperately: Height, flower number per shoot and capsule number per shoot. Moreover the variable relative fruit set (= capsule %) was determined by multiplying the number of capsules by 100 and dividing it by the number of flowers; it described the proportion of the flowers setting fruits per shoot. Beside, the mean of the counted good seeds and bad seeds per capsule has been calculated for each individual. If it was possible, 25 good seeds have been chosen and scaled. If the number of good seeds was less than 25, all good seeds have been scaled. Then the mean weight per seed for each individual has been calculated, by dividing the measured

Table 1. Measured variables and time of measurement.

measured variable	time
height/ shoot	B
flower no./ shoot	B
capsule no./ shoot	A
no. of good seeds/capsule	A
no. of bad seeds/capsule	A
weight/ good seed	A
relative fruit set/ shoot	A

B:beginning of the exclusion experiment. A:end of the exclusion experiment.

number by 25 or the total number of good seeds. In the next step, the mean, the standard deviation and the standard error concerning the mentioned variables have been calculated for each experimental group.

All mentioned values have been performed with the program SPSS 17.00 for Windows statistical software.

2.3.2 Independent Samples t-test

To test if the variables height, capsule number per shoot, flower number per shoot, number of good seeds per capsule, number of bad seeds per capsule, relative fruit set per shoot and weight per good seed are normally distributed, a *One Sample Kolmogorov-Smirnov test* was conducted. The test showed that all variables belonged to the normality distribution, which was precondition for the following t-test. The results can be found in the appendix A.

According to the first hypothesis the three populations had to be compared. Therefore an *Independent samples t- test* was used, the test compares the mean scores of two groups on a given variable. For the first issue the control groups of each population were compared concerning the variables height, number of flowers per shoot, number of capsules per shoot, relative fruit set per shoot, number of good seeds per capsule, number of bad seeds per capsule and weight per good seed. Figure 7a shows in which system the groups have been matched.

To examine the second issue, within each population the different experimental groups (control, day pollinated, night pollinated, self pollinated) have been compared with the same *t-test* as above. This time the means concerning the variables height, relative fruit set per shoot, number of good seeds per capsule, number of bad seeds per capsule and weight per good seed per capsule have been analyzed (Fig. 7b).

The test have been performed with the program SPSS 17.00 for Windows statistical software.

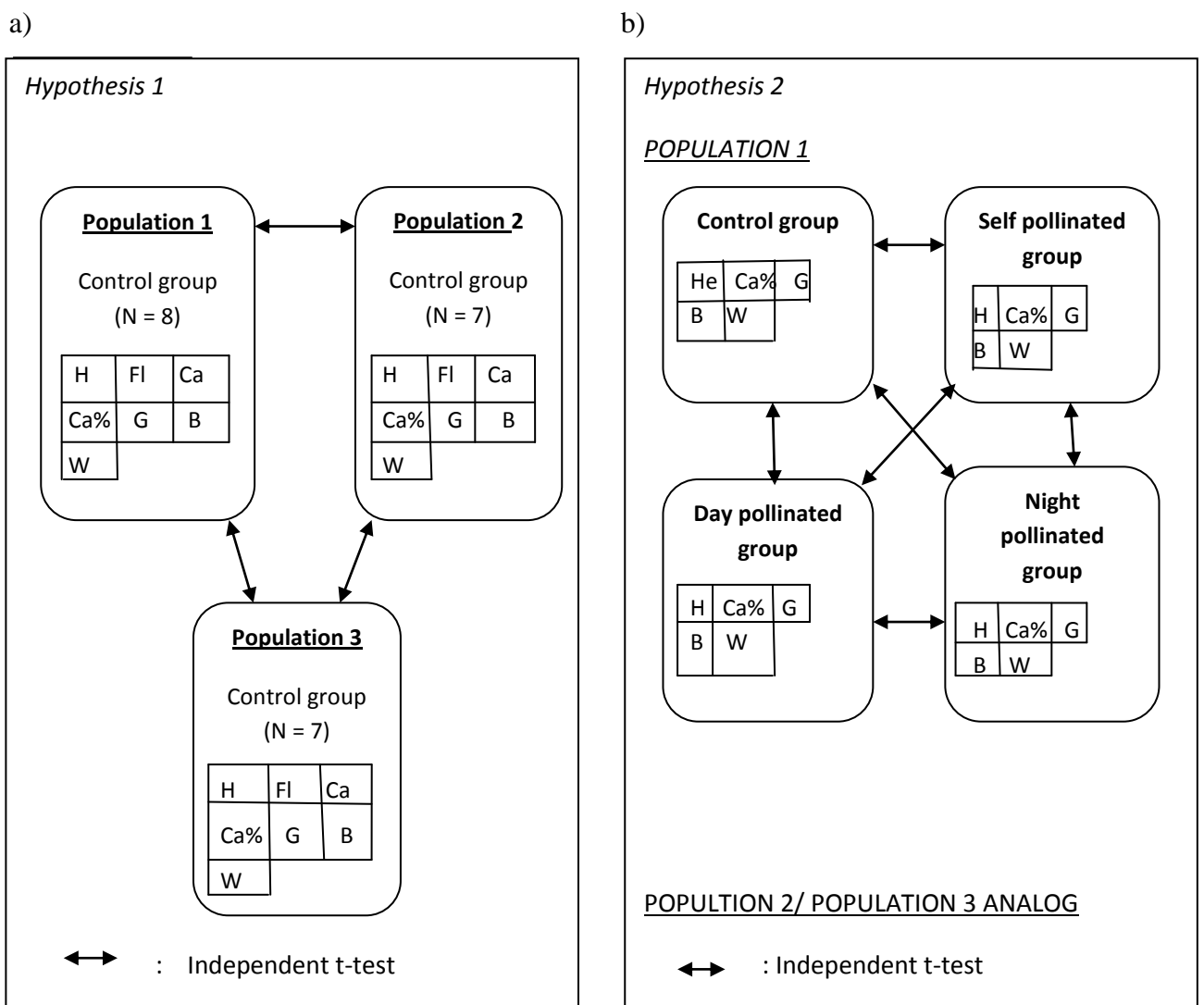


Fig. 7. Schemata of the matched groups. a) Comparison of the control groups of the populations. b) Comparison of the experimental groups within population 1, 2 and 3. *H* = height, *Fl* = flower no., *Ca* = capsule no., *Ca%* = capsule %, *G* = good seeds/ capsule, *B* = bad seeds/ capsule, *W* = weight/ good seed, ↔ = independent *t-test*.

3. Results

3.1 Description of the samples

84 plants have been measured (N = 84). The first population was represented by 29 individuals (N = 29). 8 of them belonged to the control group, 7 individuals to the day pollinated group, 7 to the night pollinated group and 7 to the self pollinated group. In the second population 28 plants (N = 28) have been measured, with the following grouping: 7 control plants, 6 day pollinated plants, 7 night pollinated plants and 8 self pollinated plants. In the third population 27 plants (N = 27) have been measured: 7 control plants, 7 day pollinated plants, 6 night pollinated plants and 7 self pollinated plants. All means, standard derivations and standard errors can be seen in the tables in the appendix B.

3.2 Hypothesis 1: Mean differences among the populations

The independent t-test showed differences concerning the variable height. On average, plants in population 1 were taller (M = 38.08, SE = 1.18) than plants in population 2 (M = 30.40, SE = 2.12) (Table 2). This difference was significant $t(13) = 3.27, p < .01$

TABLE 2. Descriptive statistics of three spatial separated populations of *Silene tatarica*. Variables: Height (cm) per shoot (No ± SE), flower number per shoot (No ± SE), capsule number per shoot (No ± SE), relative fruit set per shoot (% ± SE), number of good seeds per capsule (No ± SE), number of bad seeds per capsule (No± SE), mean weight (mg) per good seed (No ± SE).

	N	height	flower no.	capsule no.	rel. fruit set	good seeds	bad seeds	weight per seed
Population 1	8	38.08 (±)1.18	8.77 (±)0.76	6.53 (±)0.71	72.86 (±)6.03	77.46 (±)4.52	36.79 (±)10.34	0.20 (±)0.01
Population 2	7	30.40 (±)2.12	8.82 (±)0.66	6.01 (±)0.34	61.75 (±)3.28	64.75 (±)8.09	30.78 (±)2.52	0.17 (±)0.01
Population 3	7	29.84 (±)1.93	8.06 (±)0.91	3.71 (±)0.69	47.98 (±)8.93	57.36 (±)14.58	33.97 (±)7.65	0.15 (±)0.02

N = number of individuals.

(Table 3). Plants in population 3 were the smallest ($M = 29.84$, $SE = 1.93$) (Table 2). The difference to population 1 was significant $t(13) = 3.75$, $p < .01$ (Table 3). Although the number of flowers per shoot was similar among plants of the populations, the plants produced a different number of fruits per shoot: Plants of population 1 produced the most fruits ($M = 6.53$, $SE = 0.71$), plants of population 2 less than population 1 ($M = 6.01$, $SE 0.34$) and plants of population 3 produced the smallest amount, almost 50 % less capsules than population 1 ($M = 3.71$, $SE = 0.69$). The differences between population 1 and 3 ($t(13) = 2.83$, $p < 0.05$) and population 2 and 3 ($t(12) = 2.98$, $p < 0.05$) were significant (Table 3). Population 1 presented also the biggest number of relative fruit set per shoot ($M = 72.86$, $SE = 6.03$) and population 3 the smallest ($M = 47.98$, $SE = 8.93$). The t-test indicated a significant difference $t(13) = 2.36$, $p < .05$. Furthermore plants of population 1 produced the most seeds per capsule. The differences to the other populations were not significant.

Table 3. Comparison of means among the populations.

	df	t	p(2-tailed)		df	t	p(2-tailed)
height				flower no.			
Pop1 X Pop2	13	3.27	0.006**	Pop1 X Pop2	13	-0.04	0.967
Pop1 X Pop3	13	3.75	0.002**	Pop1 X Pop3	13	0.61	0.553
Pop2 X Pop3	12	0.19	0.849	Pop2 X Pop3	12	0.68	0.510
capsule no.				no. of good seeds			
Pop1 X Pop2	13	0.63	0.54	Pop1 X Pop2	11	1.43	0.181
Pop1 X Pop3	13	2.83	0.014*	Pop1 X Pop3	11	1.41	0.186
Pop2 X Pop3	12	2.98	0.011*	Pop2 X Pop3	10	0.44	0.667
rel. fruit set				no. of bad seeds			
Pop1 X Pop2	13	1.56	0.145	Pop1 X Pop2	11	0.52	0.613
Pop1 X Pop3	13	2.36	0.035*	Pop1 X Pop3	11	0.21	0.836
Pop2 X Pop3	12	1.45	0.174	Pop2 X Pop3	10	-0.4	0.700
weight per good seed							
Pop1 X Pop2	11	1.84	0.093				
Pop1 X Pop3	11	2.42	0.034*				
Pop2 X Pop3	10	1.01	0.335				

df: degrees of freedom, *t*: t-value, *p*: two tailed level of significance, *: ($p < .05$), **: ($p < .01$).

Plants of population 1 ($M = 0.20$, $SE = 0.001$) produced significant heavier seeds than population 3 ($M = 0.15$, $SE = 0.02$, $t(11) = 2.42$ $p < .05$). The seed's weight of population 2 was in between the weight of population 2 and 3.

3.3 Hypothesis 2: Mean differences among the experimental groups

Population 1:

There were not any notable differences among the mean height of the experimental groups. The control group presented the biggest percentage of relative fruit set per shoot ($M = 72.86$, $SE = 6.03$). The second biggest rate of fruit set showed the self pollinated group ($M = 68.00$, $SE = 8.81$). It can be seen that the day pollinated group presented a bigger percentage of produced fruits ($M = 61.73$, $SE = 7.03$) than the night pollinated group ($M = 48.74$, $SE = 4.75$). In Figure 8a the values can be found in a diagram. The t-test detected

Table 4. Comparison of means of fruit set and number of good seeds among the experimental groups.

	N	M	SE	df	t	p(2-tailed)
fruit set (%)				13	3.08	0.009**
control group	8	72.86	6.03			
night pollinated	7	48.72	4.75			
fruit set (%)				13	1.21	0.25
control group	8	72.86	6.03			
day pollinated	7	61.73	7.03			
fruit set (%)				13	0.46	0.65
control group	8	72.86	6.03			
self pollinated	7	68	8.81			
number of good seeds				12	2	0.071
control group		77.46	4.52			
night pollinated						
number of good seeds				12	0.87	0.4
control group		77.46	4.52			
day pollinated		72.05	4.24			
number of good seeds				12	2.55	0.026*
control group	8	77.46	4.52			
self pollinated	7	58.26	6.03			

*N: number of tested individuals, M: mean, SE: standard error, df: degrees of freedom, t: t-value, p: two tailed level of significance, *: ($p < .05$) ** ($p < .01$).*

a significant difference between the control and the night pollinated group concerning the variable relative fruit set ($t(13) = 3.08, p < .05$) (Table 4).

The comparison of the number of seeds per capsule exposed some differences: Plants in the control group produced the biggest number of good seeds ($M = 77.46, SE = 4.52$) and bad seeds ($M = 36.79, SE = 10.40$). The day pollinated group produced more good seeds ($M = 72.05, SE = 4.24$) than the night pollinated group ($M = 77.46, SE = 4.52$), but less bad seeds ($M = 30.00, SE = 2.78$) than the night pollinated group ($M = 36.79, SE = 10.40$). The seed production of the self pollinated group was relatively low compared to the other groups (good seeds: $M = 58.26, SE = 6.03$; bad seeds $M = 33.44; SE = 3.59$). The number of good seeds per capsule was significant bigger in the control group than the number of good seeds in the self pollinated group $t(12) = 2.55, p < .05$ (Table 4). In Figure 8b the values of the number of good seeds can be found in a diagram. The mean weight per good seed did not differ significantly; the night pollinated plants produced the heaviest seeds. The total results of the independent t-test can be found in appendix C.

Population 2:

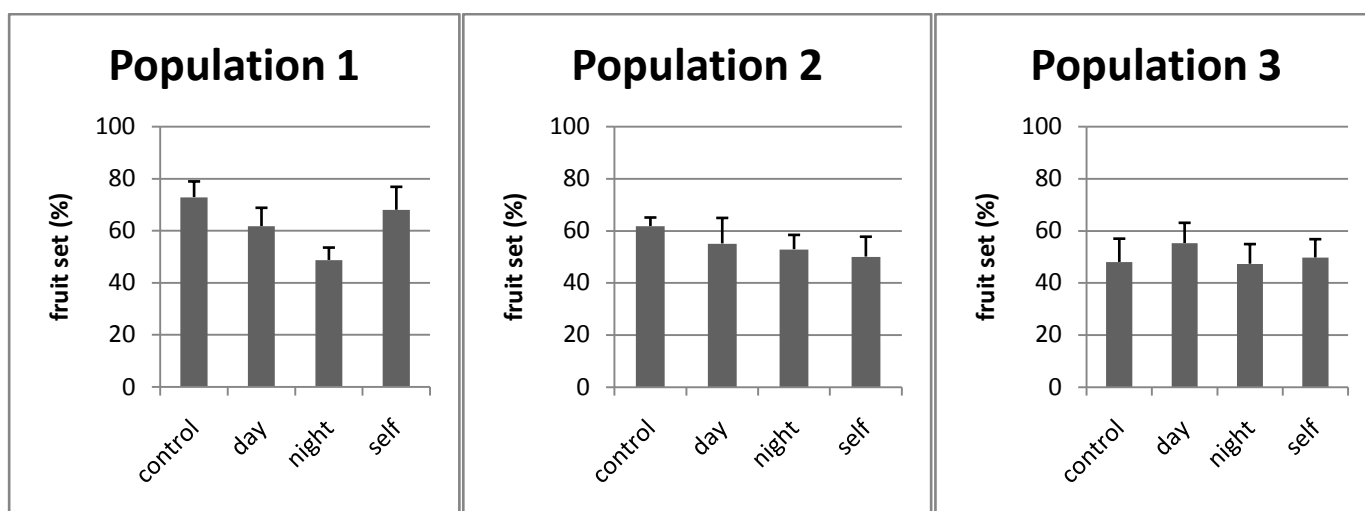
The experimental groups within population 2 did not show any remarkable mean differences. Plants of the control group showed the biggest percentage of fruit set ($M = 61.75, SE = 3.28$), the self pollinated plants the smallest ($M = 50.03, SE = 7.63$). Furthermore day pollinated plants presented a bigger percentage of fruit set ($M = 61.75, SE = 3.29$), than the night pollinated plants ($M = 52.86, SE = 5.50$). It is conspicuous, that the self pollinated plants produced the most good seeds ($M = 77.31, SE = 6.02$), while plants in the control group produced the smallest amount of good seeds ($M = 57.36, SE = 14.58$). The number of seed production of day and night pollinated plants was in between them. The night pollinated presented the heaviest seeds per capsule ($M = 0.21, SE = 0.03$) and the self pollinated plants the lightest seeds ($M = 0.17, SE = 0.03$). The values of fruit set and number of good seeds can be found in Figure 8 in a diagram. The total results of the independent t-tests can be found in appendix C.

Population 3:

The experimental groups within population 3 did not show any significant differences. The day pollinated group presented the highest percentage of fruit set ($M = 55.23, SE = 7.78$) and the night pollinated group the lowest ($M = 47.28, SE = 7.55$). Self pollinated plants showed a similar fruit set ($M = 49.70, SE = 7.01$) to the control group ($M = 47.98, SE = 8.93$).

Plants in the self pollinated group produced the biggest amount of good seeds per capsule ($M = 58.69$, $SE = 6.03$) and the night pollinated group the smallest number ($M = 55.80$, $SE = 12.51$). The night pollinated presented the heaviest seeds per capsule and plants of the control group the lightest seeds. In Figure 8 the values of relative fruit set and number of good seeds can be found in a diagram. The total results of the independent t-test can be found in appendix C.

a)



b)

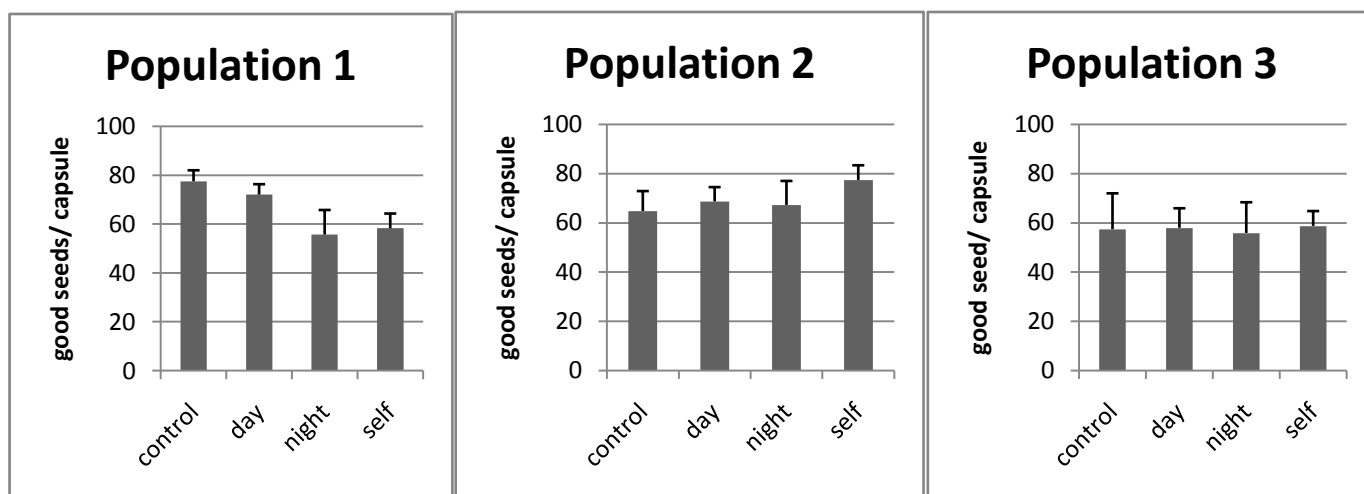


Fig. 8. Mean number and standard error ($M \pm SE$) of relative fruit set per shoot (a) and of good seeds per capsule (b) of the experimental groups of three different populations of *Silene tatarica*.

4. Discussion

Although there are some studies analyzing the pollination biology of plants of the genus *Silene*, the pollination system and the pollinators of *Silene tatarica* are still relatively unknown. *S. tatarica* propagates exclusively by sexual reproduction (Jäkäläniemi et al., 2004), thus the individuals depend on successful pollination to disperse and build new colonization. Observations suggest that diurnal pollinators are mainly bees and bumble-bees and the nocturnal pollinators are mainly represented by moths (Siikamäki, unpublished data). The plants produce a nice, not strong smelling scent (Jäkäläniemi, unpublished data), probably to attract pollinators. The inflorescences of individuals of *S. tatarica* have hermaphrodite flowers and barriers against self pollination are unknown, therefore autogamy and geitonogamy are possible alternatives to cross pollination.

The first goal of the study was to evaluate the pollination system of *S. tatarica*. In each experimental group fruit and seed production were successful, at least 50 %. It is known that populations of *S. tatarica* show high extinction and colonization rates (Jäkäläniemi et al., 2005). These facts enhance the suggestion of a generalized pollination system. Specialization is not favored because it would probably cause a minimum of propagation possibilities. In the next section the differences among the habitats and the contribution of diurnal and nocturnal pollinators to pollination success are discussed in detail.

4.1 Differences among the populations in spatial habitats

4.1.1 Mean height per shoot

The plant's height is not a direct step of the pollination process, but, nevertheless, it is a factor that can influence the plant-pollinator interaction (Fig. 2). Thus, it may play an important role in the plant-pollinator relationship. According to the "effective pollination hypothesis" the height can influence the pollinator's behavior: Plants with tall stature attract greater pollinator visitation (Donnelly, Lortie and Aarssen, 1998). Aspi et al. (2003) studied the selective forces on populations of *Silene tatarica* also in a densely, intermediately and rarely vegetated habitat. They demonstrated selection pressure concerning the height in all three different types of habitats (open, intermediate, closed). In the closed habitat the selection forces were the biggest. They suggested that the flower's visibility depends more

on the height in the closed habitat than in the other habitats. This hypothesis accords to the results of this study, plants of population 1, that grow at a densely vegetated place, showed significant taller shoots than plants of population 2 and 3 (Table 2). Probably the intra specific competition for pollinators is bigger in this habitat than in the open, rare vegetated habitats, where population 2 and 3 grow.

Beside this biotic factor there are also abiotic factors that could influence the plants' growth. To grow fast and vertically is important for individuals in a dense habitat, because the competition for light is intense (Aarssen, 1995). Probably this factor is not that important to populations of *Silene tatarica*, because the individuals grow in habitats where light is abundant, also in the dense habitat. Beside the light intensity, soil depth and provision of organic material could play a role, too. The ground may exhibit bad premises for tall statures in the open shore.

It is difficult to regard the height as attractant separately from other individual and population characteristics. Donnelly, Lortie and Aarssen (1998) found that visitors of *Verbascum thapsus* (Linné) visited higher plants more often. But they could not estimate exactly, whether this bigger rate of visitation was either a result of the height or also influenced by other factors as flower number, inflorescence number and inflorescence size (Donnelly et al., 1998).

Although the pollination visit's rates may depend on more population characteristics e. g. size and density, height is an instructive example that habitat fragmentation in *Silene tatarica* is the reason for different morphological characteristics that may influence the plant-pollinator interactions. For further studies it might be interesting to analyze the dependence of other plants' and population's characteristics on the habitat type.

4.1.2 Fruit set

The first indicator to estimate the female reproductive success in *Silene tatarica* in this experiment is the fruit production. The fact that in population 1 nearly twice the number of flowers set fruits per shoot than in population 3 and flowers of population 2 produced significantly more fruits than flowers of population 3 (Table 2 and 3) means that the fruit set is restricted in population 3. It is known that habitat fragmentation can disrupt and change plant-pollinator interactions (Neiland and Wilcock, 2002), thus the obvious explanation is that the pollinators differ among the spatial separated habitats: Probably there is a greater diversity in pollinator species in population 1 than in the habitat of population 3, and the

habitat of population 2 exhibits a greater richness of pollinator species than the habitat of population 3. It has been shown that a decrease in plant diversity is generally connected to decreases of pollination success because of pollinator and pollen limitation (Zorn-Arnold and Howe, 2007). The densely vegetated area around population 1 offers a good biotope for pollinators, it provides much food like nectar and pollen and this area is more protected concerning wind and floods. Due to absence of pollinators, visits per flower and average pollen loads per visit are less in habitat 3. Furthermore if the major pollinators are missing in habitat 3, other insects could have taken the role of pollination, with the consequence of loss in effectiveness. Besides the pollinator's behavior may also differ among the habitat types, plants of population 1 could be more attractive for pollinators and thus more visited, e.g. "effective pollinator hypothesis", than plants of population 3.

It seems that pollinator limitation is a possible explanation for pollination failure in habitat 3, but it cannot be estimated at which step of the three phases the pollination process (Fig. 1) is disrupted exactly. It could happen before or during the transfer of pollen, but failures can also occur after the deposit of the pollen: The quality of the pollen might not be good enough or the pollen quantity is insufficient, for example (Wilcock and Neiland, 2002). Moreover external factors could influence the maturing of fruits. In open shores, grazing by reindeers is very intense (Jäkäläniemi, 2004). Therefore the role of predation should also be regarded.

Plants of population 1 exhibited the biggest relative fruit set rate per individual with about 72 % (Table 2). Giménez-Benavides et al. (2007) determined in *Silene ciliata* a fruit set rate of about 86 %, while Hove (2007) described a fruit set reference of 62 % in *Silene lemmonii*. It can be suggested that the environment in the habitat of population 1 provides adequate pollination premises for *Silene tatarica*. On the opposite plants of population 3 with a rate of 48 %, advise that the habitat provides adverse premises for pollination success. Jäkäläniemi et al. (2005) reported that in open shores the risk of extinction is relatively high, but there is also the chance for new colonization. Because of these dynamics and changes in this habitat it should be difficult to develop sure plant-pollinator interactions.

4.1.3 Seed quality

Jäkäläniemi et al. (2004) pointed out that the tiny kidney shaped form is important for seed dispersal by water and gravel. Moreover seeds of *Silene tatarica* are able to germinate under water. Capsules of plants of population 1 contained more good and bad seeds than

plants of population 2; the lowest number of seeds was exhibited by plants of population 3 (Table 2). Although these differences were not significant (Table 3), it seems that visitors of *S. tatarica* in habitat 1 causes higher seed production in upper capsules than visitors of habitat 3. The reason for the loss in seed production in habitat 3 may depend on the limitation and changes in pollinators. Other studies also confirm the direct correlation between pollinators and seed production: Buide (2005) described that plants with a higher rate of pollinators visits show a higher number of seed production in *Silene acutifolia* (Fischer), for example. Another possibility is that the loss in seed set could be caused by the nutrient resources in the soil of habitat 3: The plants were not able to produce big number of seeds because of a shortage of nutrients.

The plants within population 1 produced also the heaviest seeds in the upper capsules (Table 2 and 3). Therefore the quality of seeds in upper capsules of plants in population 1 seems to be higher than seeds' quality of population 3. This enhances the suggestion of more effective pollinators in habitat 1. This point of view must be carefully regarded, because only seeds of the upper capsules have been counted: Not all capsules contain the same amount of seeds, thus it is impossible to give a suggestion about the seed production of a whole individual. Therefore the measured number of seeds in this experiment may only give a first impression of the quality of seed production caused by certain pollinators. Further studies should also regard the seed production in lower fruits.

Beside this biotic pollination, the role of self pollination and its influence on the pollination success must be necessarily regarded. A direct consequence of the absence of pollinators could cause an increasing self pollination rate in habitat 3. It has been shown that in case of pollinator limitation plants can increase their self pollination rate to minimize the loss in propagation success (Kalisz and Vogler, 2003). *Silene tatarica* may present a certain degree of self pollinated flowers. It can be suggested that the degree of self pollinated flowers increases with decreasing vegetation in populations of *S. tatarica*, the environmental conditions are inconsistent and pollinators are scarce. Selfing may provide reproductive assurance. The small number of good seeds and their weight in upper capsules promote the suggestion of self pollinated flowers. Already Darwin (1872) suggested that self pollinated flowers produce fruits with a smaller seed mass than cross pollinated flowers (Fenner and Thompson, 2005). Although the limitation of pollen and pollinators gives a reasonable explanation for seed loss, the role of seed predation should be regarded as well. This point is discussed in 4.2.1 more in detail.

4.2 Pollinator exclusion experiment

4.2.1 Population 1

Population 1 is the only population with significant differences among the experimental groups. The mean height among experimental groups did not differ significantly which suggest there should be similar attractants for pollinators concerning this variable in each experimental group. The control group, that was not treated at all, exhibited the highest percentage of produced capsules (73 %). This effect had to be anticipated because without any net treatment every pollinator can land on the flowers at any time. The fruit set in the control group was about 10 % higher than the fruit set in the day pollinated group, while the fruit set in the night pollinated group was less than 50 %. Diurnal pollinators seem to contribute quite much to fruit production; the net that enclosed the plants during day in the night pollinated group excludes important diurnal pollinators. Furthermore these numbers could be a direct consequence of shortage of nocturnal pollinators. Giménez-Benavides et al. (2007) conducted a similar experiment with a population of *Silene ciliata*. They described also a higher fruit set in the diurnal pollinated group. Furthermore previous studies showed that in general diurnal pollinators are more abundant and show higher visitation rates than nocturnal pollinators (Jennersten, 1988). Another possible explanation could be that moths are less effective in pollination, because of their mouthparts: Their long proboscises hinder them to reach the pollen. In further studies detailed analysis of the flower structures could be done to get more information weather the flowers are adapted to certain animals.

The seed quality also supports the importance of diurnal pollinators in *Silene tatarica*: The number of good seeds in the day pollinated group was comparable to the number of good seeds in the control group, while the night pollinated group exhibited an obvious smaller amount of good seeds (Fig. 8b). Through the absence of diurnal pollinators in the night pollinated group the visitation rates of minor pollinators, like small insects that are less effective and produce bad seeds, could increase. Although diurnal pollinators show higher visitation rates, several authors demonstrated that moths transport pollen more effective and farther from anther to stigma per visit than diurnal pollinators (Young, 2002; Barthelmeß, Richards and Mc Cauley, 2005); therefore nocturnal pollinators lead to higher brood size. Although the number of good seeds is smaller in the nocturnal pollinated groups, there was a tendency of nocturnal pollinators seeming to produce heavier seeds. Heavy seeds could be more advantageous for *Silene tatarica* and its seed dispersal. At this point it would be

interesting to look at the seed production in lower capsules and the seed mass of an individual as a whole. Furthermore predation could be a characteristic of the nocturnal group. Buide (2006) reported a loss of seeds in *Silene* by visitations of *Hadena*. It is questionable if nocturnal pollinators in north Finland could also take the role of predators and decrease the seed production.

In comparison to the other groups the self pollinated group showed a fruit set rate of (68 %), even more than the day pollinated group (62 %) (Table 8a). Although this group is designed to estimate the degree of self pollination, it is questionable if all of the pollinated flowers are the result of self pollination: It is possible that small insects, for example thrips, enter the net and transfer the pollen. These small insects are expected to take the role of pollination if the major pollinator dropped out (Leins and Erbar, 2008). Studies of *Silene lemmonii* (Hove, 2007) and *Silene alba* (Young, 2002) with the same experiment design also showed a very high degree of fruit set in the self pollinated group. Nevertheless it seems that the role of self pollination is not less important in *Silene tatarica*. Whether the produced fruits are caused from autogamy or geitonogamy cannot be estimated at this point.

Although the fruit set rate was relatively high in the self pollinated group, the number of good seeds was significant smaller than in the control group. Seeds within the self pollinated group also exhibited the lightest seeds. It has been shown that seeds resulting from self pollination are generally smaller than seeds resulting from out crossing (Fenner and Thompson, 2005). This result may exclude self pollination as major pollination system in *Silene tatarica*. The fact that the quality of seeds differs among the treatment groups, leads to the conclusion that the way of pollen transfer is different between control group and self pollinated group, neither self pollination nor pollination by small insects should be the major way of pollination. This suggestion concerns only upper capsules, therefore this result must be carefully regarded (see above).

4.2.2 Population 2 and population 3

Within these populations there were no significant differences in pollination success among the experimental groups (appendix C). It means that in these habitats the net does not seem to present a barrier for the major pollinators and an extreme disruption in the pollination system. The discussion in 4.2 already leads to the conclusion that pollinator diversity decreases with decreasing vegetation. Furthermore according to the “effective pollination hypothesis” these plants might not be interesting for pollinators. The absence of

pollinators or their behavior may increase the degree of self pollination in habitat 2 and 3 (4.2.3). Thus, plants within these populations may show a higher degree of self pollinated flowers than plants of population 1. Of course there is again the possibility of pollination by small insects: These animals could also exhibit the major pollinators in these habitats. These results amplify the suggestion of different, less effective pollinators in habitat 2 and habitat 3.

4.2.3 Trends that can be determined in all populations

Nevertheless some common trends can be determined in each population: It is really conspicuous that in all three populations the night pollinated plants exhibited the lowest percentage of produced capsules per shoot, only in population 2 the self pollinated group produced less fruits. Thus, in all populations, plants of the day pollinated group produced more good seeds than the night pollinated groups. On the other hand in all populations, plants of the night pollinated group produced the heaviest seeds. For the direct comparison of diurnal and nocturnal pollinators these facts amplify the acceptance that diurnal pollinators contribute more to fruit set than nocturnal pollinators.

Several studies demonstrated a greater effectiveness of nocturnal pollinators, especially moths. At this point there is the question of the seed's production optimum: Is it better to produce heavier seeds or a big number of good seeds? These measurements do not allow an estimation of one capsule's seed mass, but it can be suspected that seed mass in the night pollinated group is not coactive smaller than in the other groups, especially in population 2 and population 3. Furthermore there is the question of viable seeds. Previous studies showed that in populations of *Silene tatarica*, almost every tiny seed with a mean weight of 0.17 mg started to germinate (Jäkälänienmi et al., 2004). It can be guessed that good seeds are viable. To get knowledge about this context measurements of germination references are indispensable. Furthermore the division between good and bad seeds is questionable. A germination experiment could help again.

4.3 Conclusion and prospect

This pilot study gives a first overview about the pollination system of *Silene tatarica*, but some points must be regarded and could be improved for further studies. All in all, it seems that *S. tatarica* prefers a generalized pollination system, with visitations of different insect groups. Although it was not the goal of the study to determine the pollinators, the exact pollinators, their behavior and their visitation rates could give useful information about the pollination system of *S. tatarica*. For further studies observation of the plants and their visitors are indispensable. Furthermore this study gives only information about the female reproductive success: To get more information of the pollination process and the influence of certain pollinators on it, measurements of male reproduction could be also completed.

Hypothesis 1 can be supported, this study shows exactly that the female reproductive success in *Silene tatarica*, estimated by fruit set and seed seed, depends on the habitat. The habitat type seems to affect a variety of biotic and abiotic factors, which directly or indirectly change the composition and abundance of plants and pollinators and their relationship, and may lead to increased pollen limitation. In many experiments beside the control group there is a hand pollinated group. This group could give helpful information whether fruit set is restricted by pollen limitation or if other factors are more important.

All in all, it seems that there are nocturnal and diurnal pollinators that contribute to pollination success in *Silene tatarica*. Thus, *hypothesis 2* can be supported. Furthermore it seems that the contribution of diurnal pollinators is bigger than the contribution of nocturnal pollinators in the densely vegetated habitat of population 1. Probably diurnal pollinators are more abundant than nocturnal pollinators. Although this experiment is designed to analyze diurnal vs. nocturnal pollinators, it does not give exact information about the visitation times. At which day time stop nocturnal pollinators being active and when does the nocturnal visitation rate increase? Young (2002) observed the plants to make sure that only the wanted pollinators were active.

This method does not allow a reasonable estimation about self pollination of *Silene tatarica*. The group “self pollinated plants” could be also pollinated by small insects or ants. Because the used nets showed meshes of 2 mm x 2 mm, it was impossible to exclude all pollinators. Better results can be reached with nets consisting of smaller meshes. Another possibility to figure out the exact self pollination rate would be an analysis of genetic structures.

All in all, this pilot study gives an adequate first overview about the pollination biology

of *Silene tatarica* which can be a base for future studies. Maybe it would be better to concentrate on one population, with more plants, to get detailed information about the pollinators.

5. Abstract (English)

Pollination, the transfer of a pollen grain from the anther to the stigma, is an important step in the sexual reproduction of angiosperms. Each plant species shows an individual pollination system. Within the family of Caryophyllaceae the most species are animal pollinated and exhibit a generalized pollination system. Many studies analyze the pollinator's effectiveness and their contribution to seed set. This study analyzes the pollination system of *Silene tatarica* (Caryophyllaceae) and its pollination success depended on spatial separated habitats. Moreover the contribution of diurnal, nocturnal pollinators and self pollination is estimated.

Therefore 84 individuals of *S. tatarica* in the Oulanka National Park, Finland, have been analyzed during the flowering season 2008. The plants belonged to three different populations (dense vegetation, rare vegetation, sparsely vegetation) along the Oulanka river. To estimate the contribution of diurnal and nocturnal pollinators and the role of self pollination, plants were divided in groups and enclosed with a net during certain times. Fruit set and seed set were measured to estimate the female reproductive success. The height of each individual was measured to estimate the habitat influences on flower's structures.

The results showed that in the patchily distributed plant species *S. tatarica* height depends on the habitat type, the more densely vegetated the habitat the taller the plants are. Plants in habitat 1 are taller because height may play an important role in attracting pollinators, here. Moreover, plants growing in the densely vegetated habitat, showed a bigger female reproductive success than plants of the open habitat. Thus, the pollinator abundance seems to differ among the habitats, in the rare vegetated habitat pollination seems to be restricted by pollinator limitation. The comparison of diurnal and nocturnal pollinators detected bigger female reproductive success in day pollinated flowers than in night pollinated flowers. Diurnal pollinators may contribute more to pollination success than nocturnal pollinators. With this experiment the role of self pollination cannot be estimated exactly, nevertheless it is visible, that the absence of diurnal and nocturnal visitors decreases the pollination success.

The experiment design is useful to get a first idea of the pollination biology of

S. tatarica, but for further studies observations of pollinators are necessary for more detailed information.

6. Abstract (German)

Bestäubung ist ein wichtiger Prozess innerhalb der sexuellen Fortpflanzung bei den Bedecktsamern. In der Familie der Caryophyllaceae unterscheiden sich die Bestäubungssysteme zwischen den Pflanzenarten. Die meisten Arten werden von Tieren, hauptsächlich Insekten, bestäubt. Untersuchungen dieser Bestäubungssysteme setzen sich mit dem Verhalten der Bestäuber und ihrem Beitrag zur Frucht- und Samenproduktion auseinander. Diese Studie untersucht das Bestäubungssystem und den Bestäubungserfolg von *Silene tatarica*, in Abhängigkeit vom Habitat.

Dazu wurden Messungen an 82 Pflanzen im Oulanka Nationalpark, Finnland, während des Sommers 2008 durchgeführt. Die Pflanzen gehörten zu drei Populationen, die in drei räumlich getrennten Habitaten (kaum bewachsen, mittelmäßig bewachsen, stark bewachsen) in der Nähe des Oulanka rivers vorkommen. Durch zeitliche Abdeckung der Pflanzen mit einem Netz wurde der Beitrag von tagaktiven und nachtaktiven Bestäubern zum Bestäubungserfolg abgeschätzt, sowie der Anteil der selbst bestäubten Blüten. Der Einfluss des Habitats auf anatomische Eigenschaften der Pflanze und somit auf das Bestäubungssystem wurde exemplarisch anhand der Größe gemessen; erfolgreiche Bestäubung wurde an Frucht- und Samenproduktion abgeschätzt.

Die Ergebnisse zeigten, dass Pflanzen der Art *Silene tatarica*, die im stark bewachsenen Lebensraum vorkamen, durchschnittlich größer waren als Pflanzen in dem weniger bewachsenen Habitat. Der Konkurrenzkampf um Bestäuber ist in diesem Habitat am größten. Daraus lässt sich schlussfolgern, dass es noch andere lebensraumbedingte Eigenschaften gibt, die die Beziehung zwischen Pflanze und Bestäuber verändern könnten. Außerdem zeigten Pflanzen in dem stark bewachsenen Lebensraum die effektivste Fruchtbildung und Samenbildung, während Pflanzen, die im kaum bewachsenen Habitat vorkamen, die kleinsten Produktionsraten zeigten. Wahrscheinlich wird in diesem Lebensraum der Prozess der Bestäubung durch Bestäuber- und Pollenlimitierung eingeschränkt. Der Vergleich zwischen tagaktiven und nachtaktiven Bestäubern zeigte einen höheren Beitrag der tagaktiven Bestäuber zur Frucht- und Samenproduktion. Über den Anteil der selbst bestäubten Blüten lassen sich keine Rückschlüsse schließen, jedoch zeigte sich, dass die Bestäubung bei tag- bzw. nachtbestäubten Pflanzen effektiver war, als bei nur selbst

bestäubten Pflanzen.

Das Experiment gibt einen ersten adäquaten Überblick über die Bestäubungsbiologie der Art *Silene tatarica*, für weitere Studien ist aber eine Beobachtung der Bestäuber und deren Verhalten notwendig.



Figure 9. Blossom of *Silene tatarica* with pollinator.

(Fotograph: Matt Brewster)

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Britta

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Appendix A: Results of the One Sample Kolmogorov-Smirnov Test

Table 5. One Sample Kolmogorov-Smirnov Test.

variable	M	SD	K.-S.-Z.	p(2-tailed)
height	32.55	5.59	0.58	0.89
flower number	8.31	2.11	0.68	0.74
capsule number	4.86	1.98	0.43	0.99
capsule percent	56.18	19.48	0.49	0.97
seeds good	64.80	20.75	1.27	0.08
seeds bad	35.14	16.31	1.17	0.13
weight per seed	0.19	0.04	0.91	0.39

*M: mean of the tested normality distribution, SD: standard derivation,
K.-S.-Z. : Kolmogorov-Smirnov-Z-value, p: 2-tailed significance value.*

Appendix B: Descriptive statistics

Population 1

Table 6a. Descriptive statistics of the control and day pollinated group in population 1.

Control group	N	M	SE	SD
height per shoot (cm)	8	38.0772	1.1813	3.3411
flower number per shoot	8	8.7738	0.7634	2.1591
capsule number per shoot	8	6.5310	0.7069	1.9995
rel. fruit set per shoot	8	72.8605	6.0304	17.0566
number of good seeds per capsule	7	77.4643	4.5167	11.9499
number of bad seeds per capsule	7	36.7857	10.3957	27.5043
weight per good seed (mg)	7	0.1989	0.0086	0.0227

Day pollinated group	N	M	SE	SD
height per shoot (cm)	7	36.5488	1.3599	3.5980
flower number per shoot	7	7.8442	.61300	1.6217
capsule number per shoot	7	4.7804	.5081	1.3443
rel. fruit set per shoot	7	61.7261	7.03229	18.6057
number of good seeds per capsule	7	72.0476	4.2415	11.2220
number of bad seeds per capsule	7	30.0000	2.7796	7.3541
weight per good seed (mg)	7	0.1950	0.01600	0.0423

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Table 6b. Descriptive statistics of the night and self pollinated group in population1.

Night pollinated group	N	M	SE	SD
height per shoot (cm)	7	36.962	1.4417	3.8144
flower number per shoot	7	9.0802	0.7361	1.9474
capsule number per shoot	7	4.6526	0.4286	1.1338
rel. fruit set per shoot	7	55.7024	10.0329	26.5444
number of good seeds per capsule	7	34.4405	5.0039	13.2391
number of bad seeds per capsule	7	48.7435	4.7507	12.5690
weight per good seed (mg)	7	0.2071	0.0136	0.0359

Self pollinated group	N	M	SE	SD
height per shoot (cm)	7	36.2234	2.34721	6.21014
flower number per shoot	7	8.3350	1.10967	2.93592
capsule number per shoot	7	5.9549	.82654	2.18682
rel. fruit set per shoot	7	68.0005	8.80822	23.30437
number of good seeds per capsule	7	58.2619	6.02967	15.95301
number of bad seeds per capsule	7	33.4381	3.58770	9.49215
weight per good seed (mg)	7	.1765	.01200	.03175

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Population 2

Table 7a. Descriptive statistics of the control and day pollinated group in population 2.

Control group	N	M	SE	SD
height per shoot (cm)	7	30.3977	2.1233	5.6177
flower number per shoot	7	8.8173	0.6595	1.7448
capsule number per shoot	7	6.0131	0.3401	0.8999
rel. fruit set per shoot	6	61.7516	3.2787	8.6745
number of good seeds per capsule	6	64.7500	8.0881	19.8116
number of bad seeds per capsule	7	30.7778	2.5148	6.1601
weight per good seed (mg)	6	0.1733	00.0113	0.0276

Day pollinated group	N	M	SE	SD
height per shoot (cm)	6	28.2570	2.3567	5.7727
flower number per shoot	6	7.6944	0.7623	1.8672
capsule number per shoot	6	4.2889	0.8716	2.1349
rel. fruit set per shoot	6	55.0873	9.7880	23.9757
number of good seeds per capsule	6	68.6389	5.8196	14.2550
number of bad seeds per capsule	6	29.9167	2.7066	6.6297
weight per good seed (mg)	6	0.1878	0.0131	0.0320

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Table 7b. Descriptive statistics of the night and self pollinated group in population 2.

Night pollinated group	N	M	SE	SD
height per shoot (cm)	7	33.1017	1.5346	4.0601
flower number per shoot	7	10.1317	0.7547	1.9968
capsule number per shoot	7	5.8389	0.8289	2.1933
rel. fruit set per shoot	7	52.8603	5.4990	14.5491
number of good seeds per capsule	6	67.2083	9.7477	23.8770
number of bad seeds per capsule	6	32.0833	6.5389	16.0169
weight per good seed (mg)	6	0.2073	0.0261	0.0638

Self pollinated group	N	M	SE	SD
height per shoot (cm)	8	32.1841	1.8670	5.2805
flower number per shoot	8	9.0708	0.6414	1.8141
capsule number per shoot	8	5.1173	0.9374	2.6514
rel. fruit set per shoot	8	50.0338	7.6290	21.5781
number of good seeds per capsule	8	77.3125	6.0195	17.0258
number of bad seeds per capsule	8	36.5313	9.6362	27.2554
weight per good seed (mg)	8	0.1686	0.0266	0.0753

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Population 3

Table 8a. Descriptive statistics of the control and day pollinated group in population 3.

Control group	N	M	SE	SD
height per shoot (cm)	7	29.8410	1.9256	5.0947
flower number per shoot	7	8.0575	0.9054	2.3954
capsule number per shoot	7	3.7132	0.6925	1.8322
rel. fruit set per shoot	6	47.9802	8.9346	23.6388
number of good seeds per capsule	6	57.3611	14.5765	35.7050
number of bad seeds per capsule	7	33.9722	7.6529	18.7458
weight per good seed (mg)	6	0.1509	0.0190	0.0466

Day pollinated group	N	M	SE	SD
height per shoot (cm)	7	29.1012	1.4256	3.7718
flower number per shoot	7	6.9680	0.6663	1.7629
capsule number per shoot	7	3.8707	0.3826	1.0122
rel. fruit set per shoot	7	55.2258	7.7750	20.5707
number of good seeds per capsule	6	57.9167	7.9524	19.4793
number of bad seeds per capsule	6	39.4167	8.2557	20.2223
weight per good seed (mg)	6	0.1787	0.0101	0.0247

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Table 8b. Descriptive statistics of the night and self pollinated group in population 3.

Night pollinated group	N	M	SE	SD
height per shoot (cm)	6	28.4935	2.0148	4.9352
flower number per shoot	6	6.9739	0.9205	2.2547
capsule number per shoot	6	3.3343	0.5824	1.4266
rel. fruit set per shoot	6	47.2816	7.5463	18.4845
number of good seeds per capsule	5	55.8000	12.5054	27.9629
number of bad seeds per capsule	5	47.2833	5.4556	12.1991
weight per good seed (mg)	5	0.1930	0.0084	0.0189

Self pollinated group	N	M	SE	SD
height per shoot (cm)	7	29.4161	1.27456	3.37216
flower number per shoot	7	7.4974	.66394	1.75661
capsule number per shoot	7	3.6214	.66425	1.75744
rel. fruit set per shoot	7	49.6946	7.01095	18.54924
number of good seeds per capsule	6	58.6944	6.03423	14.78077
number of bad seeds per capsule	6	39.5833	5.54406	13.58011
weight per good seed (mg)	6	.1857	0.01526	0.03739

N : number of individuals. *M* : mean. *SE*: standard error. *SD*: standard derivation.

Appendix C: Results of the Independent Samples t-tests

Population 1

Table 9a. Comparison of means among experimental groups in population 1.

	df	t	p(2-tailed)		df	t	p(2-tailed)
height				good seeds			
G1 x G2	13	0.85	0.41	G1 x G2	12	0.87	0.4
G1 x G3	13	0.6	0.56	G1 x G3	12	2	0.07
G1 x G4	13	0.73	0.48	G1 x G4	12	2.55	0.03*
G2 x G3	12	-0.21	0.84	G2 x G3	12	1.5	0.16
G2 x G4	12	0.12	0.91	G2 x G4	12	1.87	0.09
G3 x G4	12	0.27	0.79	G3 x G4	12	-0.22	0.83
capsule %				bad seeds			
G1 x G2	13	1.21	0.25	G1 x G2	12	0.63	0.54
G1 x G3	13	3.08	0.01*	G1 x G3	12	0.2	0.84
G1 x G4	13	0.46	0.65	G1 x G4	12	0.3	0.77
G2 x G3	12	1.53	0.15	G2 x G3	12	-0.78	0.45
G2 x G4	12	-0.56	0.59	G2 x G4	12	-0.76	0.46
G3 x G4	12	-1.92	0.08	G3 x G4	12	0.16	0.87
weight per seed							
G1 x G2	12	0.21	0.84				
G1 x G3	12	-0.51	0.62				
G1 x G4	12	1.52	0.16				
G2 x G3	12	-0.57	0.58				
G2 x G4	12	0.93	0.37				
G3 x G4	12	1.69	0.12				

*G1: control group, G2: day pollinated group, G3: night pollinated group, G4: self pollinated group, df: degrees of freedom, t: t-value, p: two tailed level of significance, *: (p < .05), **: (p < .01).*

Population 2

Table 9b. Comparison of means among experimental groups in population 2.

	df	t	p(2-tailed)		df	t	p(2-tailed)
height				good seeds			
G1 x G2	12	0.68	0.51	G1 x G2	10	-0.39	0.71
G1 x G3	12	-1.03	0.32	G1 x G3	10	-0.19	0.85
G1 x G4	13	-0.64	0.54	G1 x G4	12	-1.28	0.23
G2 x G3	11	-1.78	0.1	G2 x G3	10	0.13	0.9
G2 xG 4	12	-1.3	0.21	G2 x G4	12	-1	0.33
G3 xG4	13	0.37	0.72	G3 x G4	12	-0.93	0.37
capsule %				bad seeds			
G1 x G2	11	0.69	0.51	G1 x G2	10	0.23	0.82
G1 x G3	12	1.49	0.19	G1 x G3	10	-0.19	0.86
G1 x G4	13	1.34	0.2	G1 x G4	12	-0.5	0.62
G2 x G3	11	0.21	0.84	G2 x G3	10	-0.31	0.77
G2xG4	12	0.41	0.69	G2 x G4	12	-0.58	0.58
G3 xG4	13	0.29	0.77	G3 x G4	12	-0.35	0.73
weight per seed							
G1 x G2	10	-0.84	0.42				
G1 x G3	10	-1.2	0.26				
G1 x G4	12	0.15	0.89				
G2 x G3	10	-0.67	0.52				
G2 xG4	12	0.58	0.57				
G3 XG4	12	1.01	0.33				

*G1: control group, G2: day pollinated group, G3: night pollinated group, G4: self pollinated group, df: degrees of freedom, t: t-value, p: two tailed level of significance, *: (p < .05), **: (p < .01).*

Population 3

Table 9c. Comparison of means among experimental groups in population 3.

	df	t	p(2-tailed)		df	t	p(2-tailed)
height				good seeds			
G1 x G2	12	0.31	0.76	G1 x G2	10	-0.3	0.97
G1 x G3	11	0.48	0.64	G1 x G3	9	0.08	0.94
G1 x G4	12	0.18	0.86	G1 x G4	10	-0.09	0.93
G2 x G3	11	0.25	0.81	G2 x G3	9	0.15	0.89
G2 X G4	12	-0.17	0.87	G2 X G4	10	-0.08	0.94
G3 X G4	11	-0.4	0.7	G3 X G4	9	-0.22	0.83
capsule %				bad seeds			
G1 x G2	12	-0.61	0.55	G1 x G2	10	-0.48	0.64
G1 x G3	11	0.06	0.95	G1 x G3	9	-1.36	0.21
G1 x G4	12	-0.15	0.88	G1 x G4	10	-0.59	0.57
G2 x G3	11	0.73	0.48	G2 x G3	9	-0.76	0.47
G2 X G4	12	0.53	0.61	G2 X G4	10	-0.02	0.99
G3 X G4	11	-0.23	0.82	G3 X G4	9	0.98	0.35
weight per seed							
G1 x G2	10	-1.29	0.23				
G1 x G3	9	-1.88	0.09				
G1 x G4	10	-1.42	0.19				
G2 x G3	9	-1.06	0.32				
G2 X G4	10	-0.38	0.71				
G3 X G4	9	0.4	0.7				

*G1: control group, G2: day pollinated group, G3: night pollinated group, G4: self pollinated group, df: degrees of freedom, t: t-value, p: two tailed level of significance, *: (p < .05), **: (p < .01).*

DECLARATION/ ERKLÄRUNG

Hiermit erkläre ich, dass ich die heute eingereichte Bachelorarbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie Zitate kenntlich gemacht habe. Bei der vorliegenden Bachelorarbeit handelt es sich um in Wort und Bild völlig übereinstimmende Exemplare.

Weiterhin erkläre ich, dass digitale Abbildungen nur die originalen Daten enthalten und in keinem Fall inhaltsverändernde Bildbearbeitung vorgenommen wurde.

Erstgutachter/in ist:

Als Zweitgutachter/in schlage ich vor:

Bochum, den

(Unterschrift)

